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Mangrove Forests: a Tough System to Invade but an Easy one to Rehabilitate

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Mangrove forests are tough ecosystems to invade because few species can tolerate the hydrological and edaphic conditions that prevail in mangrove habitats. The small pantropical mangrove species pool is also the basis for asserting that mangrove forests are easy to rehabilitate, at least in terms of tree species composition. The high complexity of the animal and microbial component of mangrove ecosystems is not addressed in this article. The following questions are useful as a guide for evaluating the invasion of plant species into mangrove habitats: (1) Is the invading species a halophyte? (2) What conditions of the environment is the invading species occupying and how long will those conditions last? (3) What is the geographic location of the invasion, does it penetrate the forest or is it only at the edge? (4) Is the invasion a short-term response to changes in microsite conditions? (5) Is the invasion the result of a long-term shift in the mangrove habitat?

Introduction

As a mangrove ecologist, I was surprised by the negative attitude of Hawaiians towards mangroves. Mangroves are alien species to Hawaii and because of that, their rapid establishment and expansion in those islands has caused concern among those that advocate an alien-free Archipelago. The subject of species selection (alien or native) and unintended species invasions to sites undergoing rehabilitation is a challenge to ecosystem restorationists. However, such fears should not preclude the use of alien or invasive species in rehabilitation projects because these species have advantages for rehabilitating species-rich forests in damaged sites (Lugo, 1997). But the subject remains controversial because there are strongly held views about alien species (cf. Temple, 1990; Lugo, 1990, 1992; Coblentz, 1991).

For mangrove rehabilitation in locations where mangroves are native, the alien/native species issue is not a serious problem because mangrove species are all proficient colonizers and usually can grow as long as conditions at the site remain within their range of tolerance. However, there are reports of alien species invasions into Florida mangroves, which if true, would open the question of species invasions into mangrove habitats and thus complicate the task of restoring mangrove forests.

A general model of mangrove ecosystem stress includes five types of stressors: (1) those that change the main energy source (i.e., tides, runoff, etc.), (2) those that divert a fraction of the inflow of resources to the mangroves before these resources can be used within the mangroves, (3) those that remove photosynthate before its stored or used by plants, (4) those that remove soil nutrients or mass from the system, and (5) those that affect metabolism through toxic effects (Lugo *et al.*, 1981; their Fig. 11.1). Each of these stressors has a different effect on mangroves because the disturbance force is interacting with a different ecosystem sector (i.e., canopy, soil, animals, etc.), and with different ecosystem processes (i.e., production, consumption, cycling, etc.). In general, the severity of the stress decreases from type 1 to type 5 stressors.

The mangrove stress model was used to develop a rehabilitation model for all ecosystem types (Brown and Lugo, 1994). This model depicts rehabilitation actions that reverse the conditions of the five types of stressors. For example, removing limiting factors or toxins, seeding or adding resources, restoring growth conditions, or restoring hydrological conditions or topography. In general, the cost and difficulty of a rehabilitation increases from actions that reverse type 5 stressors to those that reverse type 1 stressors. For example, it is more difficult to rehabilitate mangrove habitats (hydrology, topography) than it is to replace plants or overcome a limiting factor.

Missing from this stress model is the biodiversity attribute of mangrove forest rehabilitation. Normally, forest rehabilitation is hindered by the difficulty of directing succession through particular pathways, especially in the tropics where high species richness allow successions to proceed through multiple pathways to maturity (Ewel, 1980). However, with mangrove forests this problem is less evident because pathways for succession of mangrove species are limited in comparison with those for species-rich forests (Lugo, 1980). This is why mangroves are 'easy' to rehabilitate in comparison

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with complex lowland rain forests. When planning a mangrove rehabilitation it is possible to anticipate with certainty the species composition of the mature vegetation. However, mangrove ecosystems have complex animal communities that include marine, estuarine, and terrestrial organisms. Restoring this biotic diversity is a difficult and complex task that is not addressed here.

In this essay I address the issue of plant species invasions in mangrove forests and make the point that mangrove rehabilitation is simplified by the resistance to invasion of mangrove ecosystems. Other factors that facilitate mangrove rehabilitation are: high fecundity of mangroves, high rates of mangrove propagule dispersal, high colonizing ability of mangroves, and the continuous subsidy of tides and surface or ground water freshwater discharges. However, I recognize that there are many types of mangrove forests and some of them are very difficult to rehabilitate, i.e., dwarf mangroves *sensu* Lugo and Snedaker (1974).

Species Richness and Mangrove Invasions

Lowland tropical forests are the most species-rich forests in the world. As many as 307 tree species and 693 trees per hectare (dbh >10 cm) have been reported in these ecosystems, values that are almost equivalent to finding a different tree species with each new tree encountered in the forest (Valencia *et al.*, 1994). Under some tropical forest conditions, tree species richness is low. For example, Hart *et al.* (1989) reported species-poor forests in Africa, with values of 18 tree species per half hectare. Fewer species still are normally found in freshwater forested wetlands. Values in these forests range from 1 to 23 species per hectare with averages of 8.3 and 6 species per hectare for riverine and basin freshwater wetlands, respectively (Lugo *et al.*, 1988).

Mangrove forests are even more species-poor and in fact are among the most species-poor forest ecosystems in the tropics (Lugo *et al.*, 1988). Mangrove stands in the neotropics and the Pacific Islands can be found where the tree species list contains only one species. In fact, Jansen (1985) asked: 'Where is the mangrove understory?', after he observed that mangrove forests often contain no understory plants. Several articles were written trying to answer the questions raised by Jansen (Corlett, 1986, Lugo, 1986).

Environmental conditions within mangrove forests make it extremely difficult for non-halophytic and non-wetland plants to grow and reproduce. These include flooding, prolonged hydroperiod, salinity, anoxic conditions, and accumulation of toxic substances such as H_2S. Salinity is the major obstacle to species invasion within mangrove forests because in order to survive in a saline environment, plants must possess mechanisms to either exclude salt or mitigate its effects on living cells. Worldwide, only 34 tree species have been identified as possessing these adaptations (true mangroves *sensu* Tomlinson, 1986), 20 other species tolerate some salinity and are considered minor elements of mangroves, and an additional 60 species are considered mangrove associates (Tomlinson, 1986).

Only a small percentage of the world's flora are halophytes (plants that tolerate salinity) and those taxa with halophytic species have a lower mean number of genera per family and a lower mean number of species per genera than non-halophytic taxa (Waisel, 1972). Thus, when considering the subject of mangrove invasions by alien species, one has to realize that the species pool available to invade these ecosystems is limited. If a tree could invade the saline and hydrologic conditions of mangrove habitats, it would, by definition, be a mangrove tree species. Should this invading species be an alien to Florida or Hawaii, for example, it would not be an alien to the mangrove habitat.

Five Questions for Evaluating Species Invasions in Mangroves

The first question one should ask when finding an alien tree species or any kind of alien plant species growing inside a mangrove forest, is: *is it a halophyte*? The test for halophytism is whether or not the plant accumulates salt in their cell sap (Medina *et al.*, 1990). If it does not, the plant is not a halophyte and some other explanation must be found to explain its presence in a mangrove forest.

I have observed non-halophytes (other than epiphytes) inside mangrove forests in Florida. For example, floating aquatic plants like the water hyacinth invade mangrove forests. However, their incursions into mangroves are short-lived and depend on one of two conditions: (1) how quickly the plant dies if it floated into saline water, or (2) the residence time of the freshwater carrying the macrophyte inside the forest. Freshwater lenses occur in mangroves during periods of high rainfall or high run-off and it is possible for non-halophytic aquatic plants to occupy that ecological space and survive with the continued presence of freshwater. Once the saline condition is re-established, these invaders are doomed. So, a second question that must be answered when finding a species invasion in the mangroves is: *what conditions of the environment is it occupying and how long will those conditions last*?

Mangrove forests usually have sharp ecotones with adjacent ecosystems because the saline condition of the mangrove habitat is tidally and topographically determined (Lugo, 1980). Wherever the tide transports saltwater inland, mangroves will colonize available sediments. But slight topographic changes (in centimeters), can create a sharp ecotone where saline and tidal conditions end. Conditions beyond this ecotone either don't involve salinity, don't flood, flood without salinity, or have salinity without floods. Depending on resulting hydrology or edaphic conditions, the adjacent ecosystem can be a freshwater wetland, a saline flat, a terrestrial ecosystem, or any combination of these. The transition from mangrove to non-mangrove habitats can be sharp as indicated or gradual, where mangroves become less and less important as the salinity and tidal regime change away from those that delimit the range of mangrove growth and survival.

In Florida, I have observed alien plant species, including trees, invading the edge of mangroves. These trees were observed growing quite successfully, but failing to penetrate the mangrove habitat. Examples of these are the *Melaleuca quinquenervia, Casuarina equisetifolia*, and *Schinus terebinthifolius* (Loope *et al.*, 1994). These trees form dense and vigorous stands outside of mangrove ecotones, but fail to invade the saline soils of mangroves because they are not halophytes. Therefore, a third question one needs to address when considering the invasion of alien species into mangroves is: *What is the geographic location of the invasion, does it penetrate the forest or is it only at the edge*?

Disturbance events disrupt ecosystem structure and function, stress organisms, and can create conditions for the invasion of species. There are two principal mechanisms by which disturbances can create conditions for species invasions. First, the disturbance can alter microsite conditions on a temporal basis. For example, after gap formation in the canopy, light energy and air temperatures increase near the soil surface. Through succession, the gap gradually returns to original stand conditions. Invading species have a window of opportunity to enter the mangrove habitat during the recovery phase. *Spartina* marshes are more frost tolerant than mangroves and commonly invade an area following such a disturbance, thereby influencing species dominance (Lugo and Patterson Zucca, 1977; Kangas and Lugo, 1990).

A second mechanism by which a disturbance can affect mangrove habitats is by radically modifying the environment preventing succession back to original conditions. Instead, succession may proceed through an alternative pathway into a different ecosystem. An example would be if a disturbance changes the course of a river, or impounds a mangrove, or removes the mangrove substrate i.e., the peat. Succession after these changes is likely to proceed to different states because hydrologic, edaphic, topographic, or even salinity conditions have been so modified that mangrove trees may not be able to compete with invading tree species. Invading species have an opportunity to exploit the new environment and gain an advantage over the original mangrove species at the site. Species invasion of mangroves after a disturbance raises a fourth and a fifth question. *Is the invasion a short-term response to changes in microsite conditions*? Or *Is the invasion the result of a long-term shift in the mangrove habitat*?

Discussion

My experiences in Florida and elsewhere, suggest that alien species fail to invade mangrove forests after disturbances such as hurricanes as long as salinity and hydrologic conditions remain unchanged by the hurricane. However, it is conceivable that native or alien species could invade mangrove habitats in locations where the disturbance has changed the salinity and the hydroperiod of the stand. Smith *et al.* (1994) reported both native and alien grasses and sedges growing on the tip-up mounds inside mangroves in the months after passage of Hurricane Andrew. These elevated mounds lose their soil salt by leaching and become a different environment than at lower topography.

Human activities such as the construction of canals, diversion of water flows, construction of roads, dredging, and filling, greatly modify mangrove wetland conditions (stressor types 1 and 2 *sensu* Lugo *et al.*, 1981) and could facilitate the introduction of native or alien species into impacted mangrove habitats. In these instances it is necessary to carefully assess the environmental change, the nature of the invading species, and its spatial and temporal distribution before one can conclude that a mangrove habitat is being invaded. Such determinations are also needed to better assess if rehabilitation is called for and if so, what approach is needed to re-establish mangroves to the site.

The observations of Pimm *et al.* (1994), Loope *et al.* (1994), and Smith *et al.* (1994) after Hurricane Andrew impacted south Florida mangroves are consistent with the discussion above. The description by Loope *et al.* (1994) of the invasion of *Schinus* into 'higher (less wet and less saline) areas within the mangrove zone' deserves further analysis and an ecophysiological determination on whether this species is a halophyte or not. Pimm *et al.* (1994) suggest that *Schinus* can outgrow mangroves in open areas, but this broad generalization is not supported by the description of the phenomena in Smith *et al.* (1994). Smith *et al.* (1994) qualify their observation to 'along the upstream mangrove marsh-interface' from the Shark River to the Chatham River where *Schinus* leafed out faster than the surviving mangroves. Apparently, the 'invasion' of *Schinus* is outside the ecotone and it is not clear if this species has the capacity to invade mangrove forests.

Conclusion

Mangroves are a tough ecosystem to invade because there is a small global species pool that can survive the salinity, long hydroperiod, and anaerobic soil conditions of mangrove habitats. Even invasive species that survive one of the conditions, may not be able to survive all three. For example, *Conocarpus erectus*, listed erroneously as a mangrove, can tolerate salt but not flooding. The same is true of *Casuarina*, while *Melaleuca,* like *Pterocarpus officinalis* tolerates flooding but not salinity. Before one can conclude that an alien species has invaded a mangrove habitat one needs to answer five questions that lead one to rule out if the invading species: (1) is adapted to salinity or not, (2) is just taking advantage of a temporary environmental condition, (3) is located at a particular geographic zone avoiding the stressors of the mangrove habitat, (4) is temporarily taking advantage of a disruption of the forest by a disturbance, or (5) if the disturbance has so changed the habitat that it is no longer a mangrove environment. Because these questions have not been properly addressed in the literature, reports of mangrove invasions by alien species in south Florida may be premature.

The barriers to invasions of non-mangrove trees to mangrove habitats is an asset to mangrove rehabilitation in the neotropics. The small pool of species available for use in these environments help anticipate the species composition of mature stands and allows for the use of multiple seeding techniques followed by natural self-sorting of species according to tolerance to environmental gradients. Most of the work of rehabilitation is done by natural processes of self-design (Odum, 1988), a situation that should save resources and assure sustainability of the emerging system.

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